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Estimated genetic parameters for palatability traits of steaks from Brahman cattle^{1,2,3}

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ABSTRACT: Heritabilities and genetic and phenotypic correlations were estimated from carcass and beef palatability data collected from Brahman calves (n = 504) born in central Florida from 1996 to 2000. Traits evaluated included Warner-Bratzler shear force (after 7, 14, and 21 d of aging), panel tenderness score, connective tissue amount, juiciness, flavor intensity, and off flavor (after 14 d of aging), percentages of raw and cooked lipids, and milligrams per gram of muscle calpastatin activity. Parameters were estimated using an animal model and derivative-free restricted maximum likelihood procedures. Estimated heritabilities for d 7, 14, and 21 shear force were 0.14, 0.14, and 0.06, respectively, indicating that improvement in these traits by selection would be slow. Estimated heritabilities of sen-

sory panel attributes were 0.11, 0.12, 0.05, 0.04, and 0.01 for tenderness, connective tissue amount, juiciness, flavor intensity, and off flavor, respectively. The estimated heritabilities for percentages of raw and cooked lipids, and calpastatin activity were 0.34, 0.17, and 0.07, respectively. Most of the estimated genetic correlations among palatability traits and for palatability traits with fat thickness, marbling score, and loin muscle area were consistent with other estimates from the literature. Results indicated that improvement in tenderness based on selection for favorable shear force, sensory panel tenderness, or calpastatin activity would be slow; therefore, postslaughter intervention programs should also be considered.

Key Words: Brahman, Genetic Parameters, Palatability, Tenderness

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Introduction

Tenderness is a critical aspect of beef palatability (Morgan et al., 1991; Brooks et al., 2000). Brahmancross cattle have desirable attributes relative to reproduction and maternal traits. Researchers, however,

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have reported that beef from Brahman-cross calves is less tender than that of many Bos taurus breeds (Crouse et al., 1989), and steaks from higher-percentage Brahman cattle were less tender than those from lower percentage Brahman cattle (Johnson et al., 1990). Moderate heritability estimates from studies of crossbred Bos taurus cattle (Gregory et al., 1995; Splan et al., 1998) and crossbreds with some Bos indicus (Wheeler et al., 1996; O'Connor et al., 1997; Elzo et al., 1998) have suggested that tenderness traits would be responsive to selection programs; however, others have reported that they would not, based on low estimates of heritability (Van Vleck et al., 1992; Barkhouse et al., 1996; Wulf et al., 1996). Elzo et al. (1998), using Angus and Brahman straightbreds and crosses (0, 1/4, 3/8, and 1/2 Brahman), reported moderate heritabilities for shear force in all breed groups except straightbred Brahman. Other than that report, there is a lack of estimates for shear force of straightbred Brahmans in the literature. The distinctive appearance of Brahman-cross cattle, their widespread use in the southern United States, and their reputation for lower quality and less tender beef have made them an easy target for market discrimination by buyers. Therefore, the potential for improvement of

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²Names are necessary to report factually on available data; however, the USDA neither guarantees nor warrants the standard of the product to the exclusion of others that may also be suitable.

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beef palatability traits, particularly for traits related to tenderness, within the Brahman breed needs to be assessed. The objectives of this study were to estimate heritabilities of, and genetic correlations among, beef palatability traits and to estimate genetic and phenotypic correlations of palatability traits with adjusted fat thickness, marbling score, and loin muscle area in straightbred Brahman steers and heifers.

Materials and Methods

Carcass and palatability data of Brahman calves (n = 504; 258 heifers and 246 steers) sired by 22 Brahman bulls were collected over 5 yr (1996 through 2000) at the Subtropical Agricultural Research Station (STARS) located near Brooksville, FL. In the 1994 to 1998 breeding seasons, cows in the Brahman herd at STARS were divided into breeding herds of 30 to 50 cows, with each herd exposed for 105 d to a single Brahman sire. Calves were born in early spring of each year. They were weaned in the fall at approximately 7 mo of age. Calves were sorted by BW and gender into feedlot pens. Additional details of project design, management, and collection of carcass data were presented previously (Riley et al., 2002).

When the median backfat, as measured by real-time ultrasound of animals in a pen, was 10 mm, the entire pen was slaughtered at Central Packing Co. in Center Hill, FL. Approximately 18 h postmortem, carcasses were graded for USDA quality and yield factors. The strip loin from the left side of each carcass was removed and sent to the University of Florida Meats Laboratory, where each was fabricated into 2.54-cm-thick steaks. Steaks were vacuum-packaged in oxygen barrier bags (Cryovac B620, OTR = 30 to 50 mL 23° C⁻¹ [m²]⁻¹24 h⁻ ¹ at 1 atm; Duncan, SC), and assigned randomly to aging periods of 7, 14, or 21 d at 2°C. They were then frozen at -18°C until Warner-Bratzler shear force analyses were conducted with steaks of all aging periods or until sensory panel palatability tests were conducted with steaks aged for 14 d.

Steaks were thawed for 18 h at 4°C. A thermocouple was placed in the geometric center of thawed steaks, which were placed on Farberware Open-Hearth grills (Model 455N, Yonkers, NY). Steaks then were heated to an internal temperature of 35°C, turned, and cooked to a final internal temperature of 71°C (AMSA, 1995). After the steaks were cooled to 21°C, 6 to 8 cores (1.27 cm in diameter) were removed parallel to fiber orientation from each steak. Peak shear force was measured on each core using a Warner-Bratzler shearing device (crosshead speed = 200 mm/m) attached to an Instron Universal Testing Machine (Instron Corp., Canton, MA). Warner-Bratzler shear forces for the different aging periods were evaluated as the average of 6 to 8 shears from the same steak.

Steaks for sensory evaluation were cooked in the same manner as steaks used in shear force evaluations. After cooking, they were cut into 1.27-cm² samples and

served warm to a trained sensory panel of 8 to 10 members (AMSA, 1995). Samples were evaluated for juiciness, flavor intensity, panel tenderness, and detectable amount of connective tissue on scales of 1 through 8 (1 = extremely dry, extremely bland, extremely tough, abundant amount; 8 = extremely juicy, extremely intense, extremely tender, none detected). Off flavor of steak samples was evaluated on a scale of 1 through 6 (1 = extreme off flavor; 6 = no off flavor detected). The average of the responses of the panel were the dependent variables for statistical analyses.

Calpastatin activity was determined on unfrozen, prerigor muscle according to the procedures of Koohmaraie (1990) with slight modifications. At slaughter, a 10- to 20-g sample of the longissimus muscle was obtained from the left side of each carcass at a location just cranial to the gluteus medius. Samples were immediately frozen in liquid N and stored at -80°C until analyses. Samples were homogenized in a 2.5 volume of extraction buffer (50 mM Tris, 10 mM EDTA, and 10 mM β -mercaptoethanol [MCE], pH 8.3). The samples were then centrifuged, filtered, and dialyzed overnight (40 mM Tris, 5 mM EDTA, and 10 mM MCE, pH 7.5). After dialysis, the samples were centrifuged, filtered, and loaded gravimetrically onto anion-exchange columns (DEAE-Sephacel; Sigma Chemical, St. Louis, MO). The columns were washed with elution buffer (50 mM Tris, 1 mM EDTA, and 10 mM MCE, pH 7.5) and eluted using a linear NaCl gradient (25 to 350 mM) in elution buffer. A casein solution (100 mM Tris, 1 mM NaN₃, 5 mM CaCl₂, 5 mg/mL casein, and $1 \mu L/mL$ MCE pH 7.5) was utilized. One unit of calpastatin activity was defined as the amount of inhibitor necessary to inhibit one unit of DEAE-purified m-calpain activity.

Proximate analyses for composition were conducted on raw and cooked longissimus steaks. Steaks were ground through a 0.48-cm plate. After oven drying (Method 950.46; AOAC, 1995), total lipids were obtained on dried samples by diethyl ether extraction (Method 985.15; AOAC, 1995). Recorded weights were used to determine the percentages of moisture and lipids. The percentage of protein was determined by subtraction.

Statistical Methods

Models were built using the MIXED procedures of SAS (SAS Inst. Inc., Cary, NC). Contemporary group was confirmed as a highly significant fixed factor for all models. A contemporary group was defined as a group of calves of the same gender, fed in the same pen, and slaughtered on the same day. There were 44 contemporary groups for all traits with an average of 11.45 calves per group. Age of calf at slaughter (average of 442.7 d) was included as a linear covariate, and was important (P < 0.1 for all models) in all analyses.

Genetic parameters were estimated for animal models using restricted maximum likelihood (Boldman et

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Table 1. Unadjusted means and SD for palatability traits of steaks from Brahman cattle

Trait	n	$\overline{\mathbf{x}}$	SD	CV
Shear force (d 7), kg	503	5.58	1.93	34.59
Shear force (d 14), kg	502	5.27	1.70	32.28
Shear force (d 21), kg	504	4.82	1.61	33.40
Panel tenderness ^a	503	4.93	0.72	14.61
Connective tissue amount ^a	503	5.31	0.74	13.94
Juiciness ^a	503	5.24	0.56	10.68
Flavor intensity ^a	503	5.88	0.41	6.97
Off flavor ^b	503	5.77	0.28	4.88
Raw moisture, %	389	72.53	1.65	2.27
Raw lipids, %	461	2.98	1.46	49.08
Raw protein, %	386	23.62	1.22	5.14
Cooked moisture, %	412	61.05	3.33	5.46
Cooked lipids, %	485	5.7	2.42	42.44
Cooked protein, %	411	32.55	3.18	9.78
Calpastatin activity, mg/g muscle	490	2.69	1.17	43.40

^a Panel tenderness, detectable amount of connective tissue, juiciness, and flavor intensity measured on scales from 1 to 8: 1 = extremely tough, abundant amount, extremely dry, extremely bland; 4 = slightly tough, moderate amount, slightly dry, slightly bland; 5 = slightly tender, slight amount, slightly juicy, slightly intense; 8 = extremely tender, none detected, extremely juicy, extremely intense.

^bOff flavor measured on a scale from 1 to 6: 1 = extreme off flavor; 3 = moderate off flavor; 4 = slight off flavor, 6 = no off flavor detected.

al., 1995). The full relationship matrix was constructed by incorporation of all available pedigree data of the STARS Brahman herd and three to five generations of pedigree information for the 22 sires used in the project. Heritabilities (\mathbf{h}^2) were estimated with single-trait analyses. Starting values for the genetic and environmental variances for single-trait analyses were estimated using results from analyses (MIXED procedures) in SAS as guidelines. Single-trait analyses were run to low (10^{-3}) , and later to higher (10^{-6}) and 10^{-9} , levels of convergence. Two-trait analyses were conducted to estimate the genetic and phenotypic correlations between pairs of traits. A strategy outlined by Boldman et al. (1995) was employed for estimation of covariances and as an attempt to avoid convergence of the simplex algorithm to local maxima.

The numbers of observations and simple statistics for the traits evaluated in this study are presented in Table 1. The genetic correlations of palatability traits with adjusted (AMSA, 1995) 12th-rib fat thickness, marbling score, and loin muscle area were estimated to evaluate the potential impact of a selection program for palatability traits on EBV that affect the primary (at present) determinants of carcass value: quality and yield grade. Riley et al. (2002) reported heritabilities and correlations among these and other key carcass traits.

Results and Discussion

Heritabilities

Estimates of heritability (Table 2) for shear forces (0.14, 0.14, and 0.06 for d 7, 14, and 21 shear force, respectively) were on the low end of the range of reported estimates (0.0 to greater than 1.0) in reviews

(Marshall, 1994; Koots et al., 1994a; Burrow et al., 2001). Koots et al. (1994a) reported a weighted average of h² for shear force of 0.29, and Burrow et al. (2001) reported weighted h² averages of 0.21 from studies of Bos taurus cattle and 0.24 for studies of Bos taurus and Bos indicus straightbred and crossbred cattle. Wheeler et al. (2001) reported estimated h² of 0.29 and 0.24 for d-7 and d-14 shear force. The low estimates from the present study relative to the literature may be in part due to estimation from a single population within a single breed. Most, if not all, of reported estimates have been based upon data from crossbred cattle or from cattle of two or more breeds. However, low estimates have also been reported from such populations (Burrow et al., 2001).

The percentage of Brahman inheritance may influence the estimates of heritability for shear force. The results of Elzo et al. (1998) suggested that the heritability of shear force decreases with increasing percentage Brahman in cattle. However, Crews and Franke (1998) reported higher estimates of the heritability for shear force from data of ½ or greater Brahman steers (0.24) to 0.36) than for estimates from steers with \(\frac{1}{4} \) or less Brahman inheritance (0.02). Similarly, an Australian study (Robinson et al., 2001) reported an estimate of 0.11 for shear force in Hereford, Angus, Shorthorn, and Murray Grey, whereas that for tropically adapted cattle (Brahman, Belmont Red, and Santa Gertrudis) was 0.38. Tropical adaptation differences in cattle probably result in differences in muscle cell structure and maturation because of different nutrient intake and usage (Oddy et al., 2001); these and other forms of environmental stressors could be influential on carcass and palatability traits (Burrow et al., 2001). It could be postulated, using present results and those of Elzo et al. (1998), that tenderness may be genetically antagonistic

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Table 2. Estimates of genetic (σ_g), environmental (σ_e), and phenotypic (σ_p) SD, and heritability (h^2) for palatability traits of steaks from Brahman calves

Trait	$\sigma_{ m g}$	$\sigma_{ m e}$	$\sigma_{ m p}$	h^2
Shear force, d 7	0.456	1.136	1.224	0.14
Shear force, d 14	0.438	1.086	1.170	0.14
Shear force, d 21	0.266	1.050	1.083	0.06
Panel tenderness ^a	0.219	0.616	0.653	0.11
Connective tissue amount ^a	0.229	0.619	0.661	0.12
Juiciness ^a	0.124	0.524	0.539	0.05
Flavor intensity ^a	0.068	0.342	0.349	0.04
Off flavor ^b	0.023	0.244	0.246	0.01
Raw lipids, %	0.770	1.080	1.327	0.34
Cooked lipids, %	0.873	1.944	2.131	0.17
Calpastatin activity, mg/g muscle	0.159	0.559	0.581	0.07

^aPanel tenderness, detectable amount of connective tissue, juiciness, and flavor intensity measured on scales from 1 to 8: 1 = extremely tough, abundant amount, extremely dry, extremely bland; 5 = slightly tender, slight amount, slightly juicy, slightly intense; 8 = extremely tender, none detected, extremely juicy, extremely intense.

^bOff flavor measured on a scale from 1 to 6: 1 = extreme off flavor; 3 = moderate off flavor; 4 = slight off flavor, 6 = no off flavor detected.

with Brahman-specific adaptation to harsh tropical conditions, but this seems to be countered by the results of Crews and Franke (1998) and Robinson et al. (2001).

Postmortem intervention may affect the heritability of shear force. The low (0.06 to 0.14) estimates of h² for shear force measures on d 7, 14, and 21 (Table 2) do not adequately demonstrate the influence of aging on the degree of additive genetic control for shear force in Brahman cattle. Estimates of heritability for shear force increased with time through 35 d of aging (Wulf et al., 1996; O'Connor et al., 1997). O'Connor et al. (1997) reported breed differences in shear force after aging involving Brahman crossbred cattle; means for Bos taurus crossbred steers decreased more rapidly and to a lower ultimate value with aging than the shear force means for Bos indicus crossbred steers. Electrical stimulation may affect amounts of additive genetic variation for shear force. Exclusion of shear force data from carcasses that were not electrically stimulated resulted in a higher estimate (0.31 vs 0.19) of heritability (Johnston et al., 2001); the authors also reported higher estimates of heritability when higher voltage was applied (increase of 0.10). Electrical stimulation has been shown to accelerate proteolytic enzyme activity (Rhee and Kim, 2001). Benefits of electrical stimulation appear to be greater for Brahman or crossbred Brahman beef than for Bos taurus beef (Ferguson et al., 2000).

The low estimates (0.01 to 0.12) of h² for sensory panel traits (Table 2) were generally consistent with those from the literature. The estimate for panel tenderness of 0.11 was on the low end of a range of estimates from the literature that ranged from 0.0 to 1.0 (Marshall, 1994; Burrow et al., 2001). Weighted h² estimates for tenderness were 0.19 from studies of Bos taurus cattle and 0.23 from studies of Bos taurus and Bos indicus straightbred and crossbred cattle (Burrow et al., 2001). Wheeler et al. (2001) reported 0.22 for tenderness in crossbred cattle (including both Bos taurus and Bos indicus-Bos taurus crossbreds). The low estimates

of h^2 for juiciness score and flavor intensity agree with the low estimates (less than 0.10) reported by Wheeler et al. (2001) and the review of Burrow et al. (2001). Burrow et al. (2001) listed a range of estimates of h^2 for juiciness score from 0 to 0.70, with weighted averages of 0.20 and 0.12 from studies of *Bos taurus* cattle and studies of *Bos taurus* and *Bos indicus* cattle, respectively. The low estimates for amount of connective tissue and off flavor are apparently the first reported estimates for these traits.

Selection for decreased calpastatin activity to improve tenderness in Brahman beef seemed promising based on results of Shackelford et al. (1994a) and on the substantial differences in calpastatin activity for Brahman as compared to *Bos taurus* beef (Pringle et al., 1997; 1999). Results from the present study suggest otherwise, as the estimate of heritability for calpastatin activity (0.07, Table 2) was lower than the range of 0.15 to 0.53 reported by the review of Burrow et al. (2001).

The h² of the percentages of raw and cooked lipids (0.34 and 0.17, respectively, Table 2) were lower than the high estimates (0.50 to 0.56) from studies of crossbred cattle (Shackelford et al., 1994a; Wheeler et al., 1996; 2001). It may be possible the genetic control of the percentage of lipids in Brahman beef is lower in cooked samples. This notion was inconsistent with the results of Wheeler et al. (2001), who reported 0.51 and 0.53 estimates for the percentages of raw and cooked lipids in crossbred cattle.

The low heritability estimates for tenderness traits and for calpastatin activity indicate that response from selection for these traits would be slow. Alternative programs for improvement of tenderness may be more effective in the short term for straightbred Brahman cattle. This conclusion should be limited to longissimus steaks; there is growing evidence that tenderness in other muscles is not strongly genetically related to longissimus tenderness (Johnston et al., 2001; Robinson et al., 2001).

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Table 3. Estimates of genetic and phenotypic correlations for palatability traits of Brahman cattle^a

1	2	3	4	5	6	7	8	9	10	11
	0.44	0.57	-0.41	-0.39	-0.11	-0.05	0.02	-0.07	0.03	0.14
0.79		0.47	-0.41	-0.38	-0.14	-0.11	0.00	-0.04	-0.01	0.10
0.95	1.00		-0.39	-0.37	-0.12	-0.05	0.00	-0.12	-0.03	0.12
-0.72	-0.8	-0.71		0.88	0.42	0.23	0.02	0.00	0.11	-0.10
-0.33	-0.67	-0.63	1.00		0.31	0.20	0.00	-0.02	0.08	-0.08
-0.88	-1.00	-1.00	1.00	1.00		0.52	0.04	0.03	0.09	0.05
-0.61	0.13	-1.00	-0.39	-0.06	-0.67		0.19	0.05	0.01	0.03
0.21	0.04	0.45	-0.87	-1.00	-0.52	1.00		0.03	-0.08	-0.05
0.45	0.39	0.41	-0.09	-0.09	-0.22	0.48	0.65		0.26	-0.05
0.29	-0.08	-0.29	-0.07	-0.09	0.38	0.58	1.00	0.93		-0.04
0.73	0.06	1.00	0.67	0.55	-0.34	-1.00	-1.00	0.30	0.11	
	0.95 -0.72 -0.33 -0.88 -0.61 0.21 0.45 0.29	0.44 0.79 0.95 1.00 -0.72 -0.8 -0.33 -0.67 -0.88 -1.00 -0.61 0.13 0.21 0.04 0.45 0.39 0.29 -0.08	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	$\begin{array}{c ccccccccccccccccccccccccccccccccccc$

^aGenetic correlation estimates are below the diagonal; phenotypic correlations are above the diagonal.

Correlations

Interpretation of the estimates of correlation (Table 3) presented here should be tempered by considering the relatively small sample size for the study and the low estimates of heritability of many of the individual traits. The estimates of the genetic correlations of shear force with other panel sensory traits were, in most cases, consistent with estimates from other studies of these traits (Van Vleck et al., 1992; Gregory et al., 1995; Wheeler et al., 1996; 2001). Estimates of genetic correlation for percentage lipids with other traits related to palatability were within the reported range of estimates (Shackelford et al., 1994a; Wheeler et al., 1996; 2001). The estimates involving off flavor and connective tissue amount with the other sensory panel traits are apparently the only reported estimates for these traits. Estimates of genetic correlation for calpastatin activity with the other traits of this study were generally large and consistent with those reported by Shackelford et al. (1994a) and O'Connor et al. (1997), although some from the latter study were of a slightly lower magnitude.

The estimates of genetic correlation for flavor intensity with tenderness score and with juiciness score were large and negative, in contrast to large, positive reported estimates from other studies (Van Vleck et al., 1992; Gregory et al., 1995). Although there are many differences between these and those of the present study, the large standard errors of the estimated correlations in all three studies probably account for most of the differences.

Phenotypic correlations for pairs of traits are presented above the diagonal in Table 3. Most were similar to those reported in the literature (Wulf et al., 1996; O'Connor et al., 1997). An exception was the estimate for beef flavor intensity and juiciness (0.51), which was larger than reported low estimates (Van Vleck et al., 1992; Gregory et al., 1995; Wheeler et al., 2001). In general, the estimates of phenotypic correlation were also consistent with simple or residual correlations for

various pairs of palatability traits that have been reported (Shackelford et al., 1995; Sherbeck et al., 1996; Wulf et al., 1997). The phenotypic correlations of calpastatin activity with the other traits were consistent with simple correlations reported by Wulf et al. (1996) and Pringle et al. (1997), but of smaller magnitude than the majority of correlations from the literature (Whipple et al., 1990; Sherbeck et al., 1996; O'Connor et al., 1997).

The moderate to large estimates of genetic and phenotypic correlations among the sensory panel palatability traits (and those of Van Vleck et al., 1992 and Gregory et al., 1995) seem to indicate interdependency among these traits. The most desirable ratings for flavor intensity probably vary among consumers. The panel tenderness, connective tissue amount, juiciness, and off-flavor scales, however, clearly have "good" vs "not good" scores. It seems reasonable to assume that samples rated for multiple traits would tend to be either mostly favorable or mostly unfavorable (or at least a sample rated with poor scores for one trait would also tend to be rated unfavorably for the others, since the connective tissue amount and off-flavor presence are subjective measurements of unfavorable attributes). Norman (1982) suggested that tenderness influenced juiciness scores. Shorthose and Harris (1991), in a discussion of the relationship between tenderness and juiciness, called this the "halo" effect. Perry et al. (2001) suggested, as a possible explanation of this effect, that postmortem changes in muscle may jointly affect both traits. The experience and/or training of sensory panel members may be responsible to some degree for its occurrence.

The estimates of genetic correlation of the palatability traits of this study with adjusted fat thickness, marbling score, and loin muscle area (Table 4) were generally consistent with previous studies (Marshall, 1994; Koots et al., 1994b; Burrow et al., 2001). Different estimates included large positive estimates for fat thickness with tenderness, juiciness, and flavor intensity (Wheeler et al. 2001), and moderate to large positive

^bPanel tenderness, detectable amount of connective tissue, juiciness, and flavor intensity measured on scales from 1 to 8: 1 = extremely tough, abundant amount, extremely dry, extremely bland; 5 = slightly tender, slight amount, slightly juicy, slightly intense; 8 = extremely tender, none detected, extremely juicy, extremely intense.

[°]Off flavor measured on a scale from 1 to 6: 1 = extreme off flavor; 3 = moderate off flavor; 4 = slight off flavor, 6 = no off flavor detected.

Table 4. Estimates of genetic (r_g) and phenotypic (r_p) correlations between palatability traits and adjusted 12th-rib backfat thickness, marbling score, and loin muscle area in Brahman cattle

	Fat thickness		Marbling score		Loin muscle area	
Trait	\mathbf{r}_{g}	$ m r_p$	$ m r_{g}$	r_{p}	$ m r_{ m g}$	\mathbf{r}_{p}
Shear force, d 7	0.14	-0.02	0.13	0.02	0.67	-0.03
Shear force, d 14	0.24	-0.05	0.36	0.01	-0.08	-0.05
Shear force, d 21	0.54	0.02	0.19	0.05	0.20	-0.02
Panel tenderness ^b	-0.26	0.17	0.23	0.02	-0.13	0.02
Connective tissue amount ^b	-0.12	0.02	0.06	-0.02	-0.11	0.05
$Juiciness^b$	-0.20	0.01	-0.58	0.08	-0.65	-0.04
Flavor intensity ^b	0.20	0.04	-0.45	0.01	-1.00	-0.04
Off flavor ^c	0.22	0.01	-0.43	0.05	-0.91	-0.02
Raw lipids, %	0.58	0.18	0.73	0.36	0.14	0.14
Cooked lipids, %	0.70	0.26	0.76	0.41	0.23	-0.01
Calpastatin activity ^d	0.07	-0.05	0.27	0.03	0.52	0.07

^a200 to 299 = traces; 300 to 399 = slight; 400 to 499 = small.

estimates of marbling score with juiciness and with flavor intensity (Van Vleck et al., 1992; Gregory et al., 1995; Wheeler et al., 1996; 2001).

The relationships between "maturation" type traits, including traits related to fat deposition and muscle growth, and palatability traits (tenderness) in Brahman cattle may warrant additional consideration. Much of the previous work shows that phenotypes and EBV for tenderness and intramuscular fat deposition tend to be positively related (i.e., more tender, more fat, and vice versa), with the same holding true for intramuscular fat deposition and sensory juiciness scores in most cattle populations. Although the results of the present study could only be considered suggestive at best, the estimates of genetic correlation for shear force with percentage of raw lipids (Table 3) and for shear force with fat thickness and marbling score (Table 4) may indicate the possibility that a unique fat-tenderness relationship exists in Brahman cattle. Although it is generally accepted that marbling score accounts for less than 10% of variation in tenderness (Shackelford et al., 1994b; Wheeler et al., 1994), fat is probably the most variable carcass component, and its presence affects tenderness in certain muscles in conjunction with rate of chilling (Shorthose and Harris, 1991), or in interaction with the connective tissue matrix (Nishimura et al., 1999). A unique fat-tenderness relationship in Brahmans does not seem unreasonable because of the substantial set of differences in most traits between Bos taurus and Bos indicus cattle. Further investigation is needed to determine the existence and usefulness of such a relationship, or to see if it is merely a consequence of sampling error or of later fat deposition associated with later physiological maturation.

Implications

The estimates of heritability for traits related to tenderness in Brahman cattle, including Warner-Bratzler shear force, postmortem calpastatin activity, sensory panel tenderness score, juiciness score, and amount of connective tissue, were low and indicate that selective improvement of these traits would be slow. Selection should be complemented by postslaughter interventions for tenderness improvement. The interaction of genetics with these intervention techniques should be investigated.

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^bPanel tenderness, detectable amount of connective tissue, juiciness, and flavor intensity measured on scales from 1 to 8: 1 = extremely tough, abundant amount, extremely dry, extremely bland; 5 = slightly tender, slight amount, slightly juicy, slightly intense; 8 = extremely tender, none detected, extremely juicy, extremely intense.

[°]Off flavor measured on a scale from 1 to 6: 1 = extreme off flavor; 3 = moderate off flavor; 4 = slight off-flavor, 6 = no off flavor detected.

^dCalpastatin activity measured as mg/g muscle.

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